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POSSIBLE MOTION DETECTION IN THE VERTEBRATE MIDDLE EAR

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INTRODUCTION

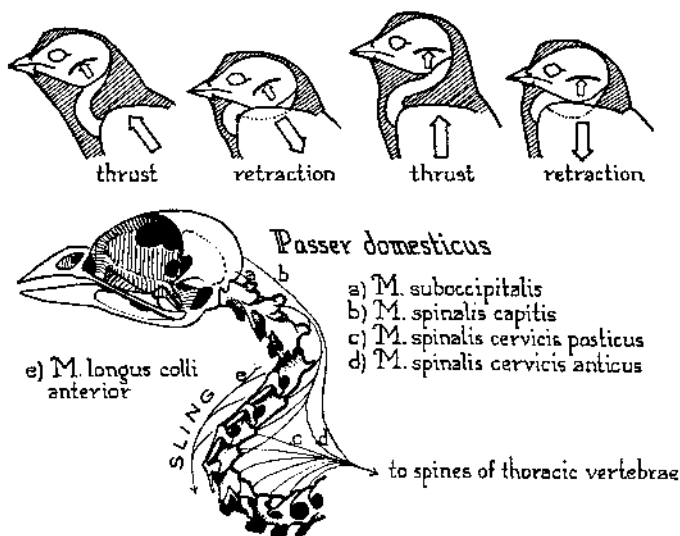
The functional anatomist working with vertebrates may well feel that the middle ear is not satisfactorily explained by ascribing to it a hearing function alone. The observed broadening into vane-like surfaces, of the columella in birds and the malleus in most mammals, is not called for if they exist only to reduce sound waves, reaching the tympanum, to vibrations in the inner ear. This paper seeks to show that these vanes have air sinuses directed toward them and that air impacts against the vanes, resulting from rapid movements of the animal, may rock the foot plate in the *fenestra ovale*.

The orientation of vanes in the precise planes to intercept such air shifts as must be set up by the normal thrusting movements of the particular species in hundreds of cases, is hardly ascribable to chance. It is suspected that the apparatus forms the basis for an accessory motion sense, based on the inertia of air, supplementary to the rotational sense of the semicircular canals, based on the inertia of fluid. It is postulated that this sense would report thrusting motion via the *papilla basilaris* of the cochlea, without disturbing the predominant hearing function.

GENERAL OBSERVATIONS

It is the method of functional anatomy to try to correlate the observation of unusual activity in a species with peculiarities of structural design. A motion-detecting role of the middle ear was first suspected when it was observed that many groups of small birds and mammals, having greatly enlarged air sinuses in the middle ear region, display activity demanding exceptional balance. The correlations occur convergently in at least eight groups of ricochetal mammals (e.g. jumping jerboas) and in foraging birds (e.g. food-scratching towhee) . The anatomical background is enlarged on below.

Birds differ from other tetrapod vertebrates in the long, flexible neck with many vertebrae. Böker (1938: 65 ff.) has mentioned this S-shaped neck and the muscular "sling" of its ventral flexure for straightening it—and this is almost as characteristic of passerine birds as of the heron-like species figured by him. A diagrammatic representation of the neck in the English sparrow (*Passer domesticus*), based on the work of Vallois (1922), shows approximately the arrangement of the *M. spinalis* and its parts, for shortening the neck by increasing the curvature (fig. 1). The complicated arrangement of the *M. longus colli anterior* for lengthening it, by straightening, cannot be shown adequately in such a diagram, but its mechanics is indicated by the arrow labeled "sling."



THRUST AND RETRACTION MECHANICS

Figure 1. THRUST AND RETRACTION MECHANICS. A diagrammatic representation of the parts of *M. spinalis* for shortening the S-shaped neck (after Vallois). The complex arrangement of *M. longus colli anterior* for lengthening it by straightening is indicated by the arrow labeled "sling."

Such an arrangement obviously permits the maximum of flexibility in the head-region of birds. I long ago pointed out (Beecher, 1951, 1962) that birds always hold the head level in flight, even when the body turns and twists in steep bank-

ing maneuvers. It is also a matter of observation that, in hopping locomotion, the neck tends, reflexly, to absorb some of the movement, so that the head rides on a more even plane. But it is a combination of this morphological arrangement and high metabolism that permits the extremely rapid head movements marking the ceaseless activity of birds.

The abruptness of these movements needs to be emphasized. When viewed through binoculars at very close range, every head-movement of a passerine bird, however imperceptible in amount, is sudden or abrupt. Such of these movements as are rotational in nature, by virtue of neck origin close to the skull—momentary movements of a cocking sort—are probably reported adequately to the brain by the semicircular canals. Thus, the head rotates in some plane and the fluid in the canals concerned with that plane remains behind, causing apparent flow and stimulation of the ampullae, which ceases with the movement. This has been the only known momentary *motion* sense. Changes of head *position* or attitude of longer duration are reported by the gravity-system of the otolith organs so long as they remain in effect. But this leaves a whole class of momentary movements of the bird's head possibly not adequately reported by any known motion sense. These are the non-rotational, thrusting movements involving the whole neck (*fig. 1*).

For example, a common method of feeding seen in the brown thrasher (*Toxostoma rufum*), robin (*Turdus migratorius*) and thrushes makes use of an *arrested head thrust*. A robin runs along on the lawn for a short distance with the head more or less lowered, then suddenly stops, simultaneously thrusting the head upward. If it sees a worm it thrusts the head forward and downward and snatches it. These thrusting movements are rapid and straight, their termination abrupt. The *head retraction* or withdrawal to the normal rest position in the first instance and the tugging movements in extracting the worm in the second, are also non-rotational and abrupt.

A consideration of the mammals shows them to be also characterized by rapidity of motion, sometimes of the body as a whole in running, sometimes only of the head in slower locomotion and feeding. The ricochet of jerboas, kangaroo

rats and elephant shrews exemplifies the former ideally. However, since mammals, despite the varying length of the neck, almost universally possess only seven cervical vertebrae, they cannot compare with birds for flexibility of head movement. Yet carnivores in tearing at food, and herbivores in tearing off grass, all exhibit movements of short excursion but rapid acceleration. Less abrupt are the swinging and bobbing movements of the head in normal locomotion, but the higher Primates, including man, is almost the only group of mammals incapable of a feeding movement involving some suggestion of the thrust and retraction of the head noted in birds. This lack seems to be correlated with forward vision and the habit of bringing food to the mouth manually. It is virtually the only group not exhibiting head-bobbing in rhythm with locomotion.

A consideration of the auditory ossicles of most mammals other than the higher Primates shows the malleus to have its processes expanded into thin bony vanes, so placed as to impede momentary air currents in the tympanic cavity. The functional analogue is seen in birds in the vane-like expansion of the bony columella and the cartilaginous extracolumella. In lizards, turtles, frogs and snakes, membranes securing the rod-like columella to the wall of the tympanic cavity and to the drum, may serve as vanes. In fish and salamanders the absence of both auditory ossicles and tympanic cavity prevent a functional comparison with higher vertebrates.

Before going into a family by family survey of the middle ear in the vertebrate classes, let us consider the elementary physics involved in these thrusting-retracting movements, which we may think of as accelerations and decelerations. If a closed vessel of air is moved suddenly forward, there will be a momentary rush of air to the rear wall inside. Of course this is only apparent, the air being really left behind on account of its inertia. It is also only momentary, pressure within the vessel becoming uniform on all walls as soon as the acceleration becomes constant. But now a sudden arrest of forward motion or deceleration will produce a similar pressure on the forward wall. The middle ear or tympanic cavity of vertebrates is a chamber containing air, and the auditory ossicles of mammals and their equivalents in birds and lower vertebrates should be sensitive to accelerations and decelera-

tions of air, set up during typical activity.

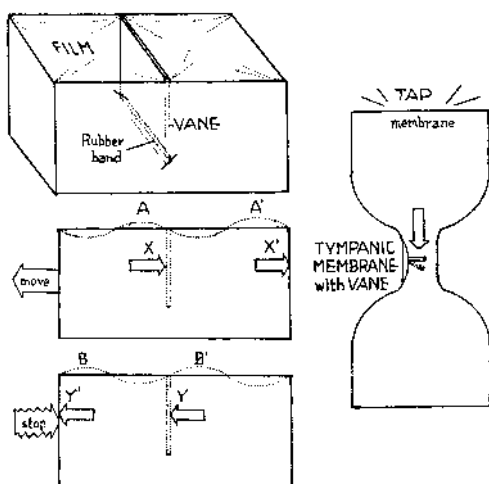


Figure 2. ACCELERATION EFFECTS OF AIR IN A CLOSED CONTAINER.

Simple, enlarged models show the behavior of air in a closed container. A cardboard box, 8x8x12 inches, may be fitted with a top of polyethelene film one-fourth mil thick, taped on with scotch tape. A light vane of polyurethane, 4x7³/₄ inches is taped to the inside surface of the film with double-stick scotch tape and suspended in space between the two strands of a rubber band secured to the box walls (*fig. 2*). When this box is accelerated a foot or so along its long axis and then halted, the film, slack enough to have a downward belly to either side of the vane, confirms the predicted behavior of confined air under acceleration and deceleration. With an initial acceleration of the box to the left, the film bellies upward at A and A', indicating the pressure of air on vane X and rear wall X'. Upon deceleration, the film bellies upward at B and B', indicating air pressure at Y and Y'. XY represents the two surfaces of the vane, standing in for the manubrium of the malleus in the mammalian middle ear or the extracolumella of the avian middle ear.

To more nearly imitate the funneling of the highly inflated bullae of the kangaroo rat into the constricted middle ear

cavity, two rigid plastic bottles were joined at the necks and cut out to receive a small taped-on polyethylene tympanic membrane. A small polyurethane vane was attached on the inside (*fig. 2*). To provide a means of creating air impacts on the vane without moving the system, the top bottle was fitted with a polyethylene membrane. A light tap on this membrane caused the vane to fly violently in the opposite direction, confirming the supposition that funneling a large body of air to a small passage increases the impact.

AIR VANE MODIFICATIONS OF THE EAR IN BIRDS

The great variety of form in the *columella* of birds may be appreciated at a glance from Krause's (1901) plates, although the lack of uniformity in orientation makes comparisons impossible. In general we find in birds (as in mammals) that degree of vane development and associated air mass is in direct relation to activity. The more generalized birds like the common fowl (*Gallus domesticus*) do not have the shaft of the bony columella expanded and flattened, although the cartilage head of the columella in actual contact with the drum is so modified. As stated by Pohlmann (1921) this "extracolumella" displays three vanes held out, sail-like, by ligaments from the walls of the tympanic cavity (middle ear) in planes at about right angles to each other. In *Gallus* the associated air mass is minimal, the middle ear of each side opening into the oral cavity via a definite eustachian tube, constructed through the cancellous bony tissue of the basitemporal region (*fig. 3*). More advanced and active passerine species, such as the emberizine finch, the towhee (*Pipilo*), have the shaft of the columella itself vastly flattened as a vane—and

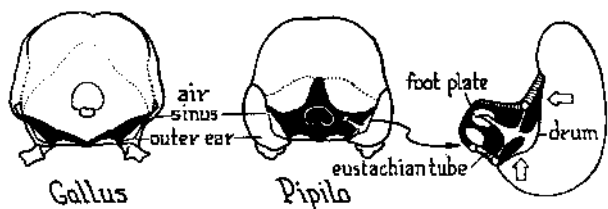
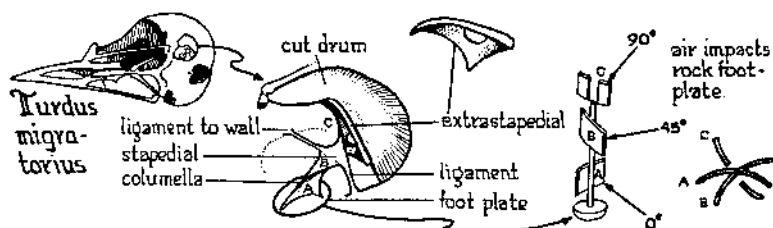


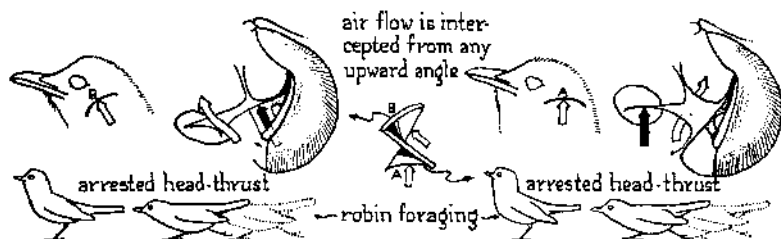
Figure 3. ADAPTIVE INCREASE IN AIR SINUSES. In the domestic fowl (*Gallus*) the middle ear communicates with the oral cavity by a definite, bony eustachian tube. In the towhee (*Pipilo*), an active emberizine finch, the eustachian tube is in an open communication with the basitemporal air sinus, vastly increasing the air mass (black) acting on the vane of the columella.

the eustachian tube, while still entering the oral cavity, is in open communication with a hollowed out basitemporal air sinus in which cancellous structure has disappeared but for a few trabeculae.

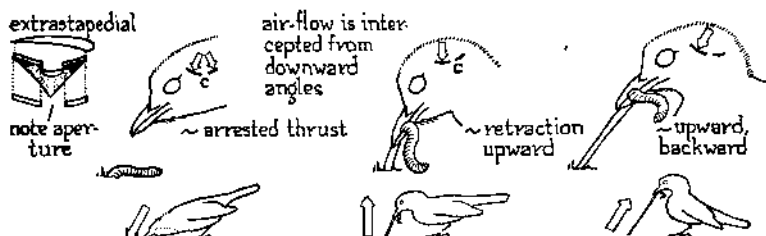
Air Vanes of the Middle Ear in Passerine Birds.—The postulated function of the air vanes is most readily grasped in the highly evolved form seen in such a passerine species as the robin (*Turdus migratorius*). The bony wall of the external ear and part of the drum have been cut away in fig. 4, revealing the functional parts of the middle ear, delicately



AIR VANES OF THE MIDDLE EAR



EFFECT OF 45° TORSION OF COLUMELLA



EFFECT OF APERTURE IN EXTRASTAPEDIAL

suspended by ligaments originating on the surrounding walls or tympanic ring. If this figure is compared with that of Pohlmann for the common fowl, many changes will be seen to have occurred—not the least being a fusion of parts in the cartilaginous *extracolumella*. The *supra-* and *infra-stapedial* of the latter are so fused that I have taken the liberty of referring to both in my figure as merely *stapedial*. The columella, of thin bone, convexly flattened and twisted, joins with the cartilaginous stapedial almost imperceptibly to form the air vanes A and B. The cartilaginous air vane C is the *stapedial*, in actual contact with the drum, and responsible for its tent-like outward umbo when viewed externally. Since it lies in a plane at 45° (approx.) to that of vane B and since vanes A and B have undergone torsion through 45° , these three vanes could be schematically represented in cross section as shown on the extreme right in the figure.

The net effect of this arrangement of three vanes on a single axis, oriented roughly in planes of 0° , 45° and 90° , would be the interception of momentary air currents resulting from motion in these three directions—these currents rocking the *columellar foot-plate* in a different axis for each direction. Since the foot plate is suspended in the *fenestra ovale* by the *ligamentum annulare*, a stimulus should be imparted to the lymph of the inner ear which the *papilla basilaris* in the cochlea may be able to distinguish from that produced by sound waves striking the drum.

Effect of 45° Torsion of the Columella.—As a result of the convexity and torsion of the columella and stapedial, the vanes A and B lie in planes at a 45° angle to each other. In the figures of the foraging robin and its arrested head-thrust, it is shown that the orientation of these vanes in the head would be such as to intercept air movement upward and forward. Since these vanes are convex dorsally and anteriorly, air impacts downward and backward would have far less effect. Therefore, when the head thrust is upward and forward, its arrest results in air impact on vane B ; when the thrust is straight upward, its arrest results in air impact on vane A. Due to the torsion or twisting, intermediate directions of impact could, theoretically, be distinguished by a different axis of

rocking of the foot-plate in the fenestra ovale.

Figure 4. FUNCTION OF AIR VANES IN THE MIDDLE EAR OF BIRDS.

Effect of the Aperture in the Extrastapedial.—Vane C, represented by the extrastapedial, is smaller but more effective, since it is in contact with the inner cone-like surface of the drum. This vane lies in a plane at about 45° to that of vane A and 90° to that of vane B (This is a rough estimate. In most passerines the range of these three vanes appears to be nearer 100°). The aperture in the extrastapedial may cause it to function as two vanes. It may receive air impacts due to arrested downward thrusts and retractions upward and upward-backward, such accelerations as a robin's middle ear would experience in the extraction of a worm from the ground. As the pull shifted to a more backward direction, the impact might shift to vane B.

Orientation of the Vanes in Different Species.—I have earlier shown (Beecher, 1951) that all birds, and other vertebrates as well, have characteristic attitudes of the head in rest—positions presumably held with the minimum of muscular strain. In virtually all cases this is the position in which the external semicircular canal is horizontal and, with this as a criterion, it is clear that rather startling differences have occurred in the space orientation of the skulls of even closely-related genera. Almost all the figures in this paper show the heads of animals in their correct orientation, as determined by correlating observation with the position of the canals in the skull. In fig. 5, it may be seen that, for the blackbird family (*Icteridae*) in this normal rest position, the cowbird (*Molothrus*) and grackle (*Quiscalus*) hold the bill somewhat elevated, whereas the redwing (*Agelaius*) holds it somewhat depressed. Orioles (*Icterus*) would be somewhat intermediate in position.

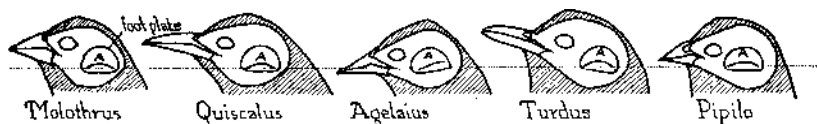


Figure 5. VANE A IN NORMAL POSITION. With birds in rest attitude (external semicircular canal horizontal), downward rotation of the foot plate is seen in *Agelaius*, upward rotation in *Turdus*. Vane A, varying independently, tends to orient in the horizontal plane.

Since the cowbird is regarded as ancestral in the Icteridae (Friedmann, 1929, Beecher, 1950, 1951b, 1953), we may perhaps view the skulls of the redwing and oriole as indicating a

rotation downward (counterclockwise) , viewed from the left side. The canals, being in the same space orientation in all (with the external canal horizontal) , give the impression of having remained behind, while the rest of the ear has followed the rotation. The flattened ventral border of the *fenestra ovale* (which the foot plate closely fits) is, for example, no longer horizontal as it was in the cowbird and grackle, but is angled downward somewhat in the redwing and oriole. Moreover, the expanded columella, arising from the foot plate as vane A is angled still more out of the horizontal in possible agreement with more forward direction of upward head movements in the redwing and oriole. On the other hand, the foot plate is angled slightly upward in the robin (*Turdus*), suggesting that the skull has rotated upward in this species which carries the bill notably elevated. Here vane A emerges from the foot plate at a downward angle with the result that it is really horizontal—as it is in nearly all species possessing this vane. This tendency for vane A to be horizontal, whatever the angular variations of the foot plate, seems to indicate positive selection on the vane insuring that it will be transverse to air impacts directly upward, despite rotations that have occurred either in the foot-plate or the total skull. The situation existing in the towhee (*Pipilo*)—*with* external canal, foot plate and vane A all roughly horizontal—is typical of the great majority of passerines.

Conversely, it is a general rule in at least the larger non-passerines for the foot plate to be rotated counterclockwise (viewed from the left) , with respect to the horizontal external canal, and for vane B (vane A is most often missing) to rotate still farther in this direction. As seen in *fig. 6*, its tendency is to occupy a vertical plane in space—transverse to

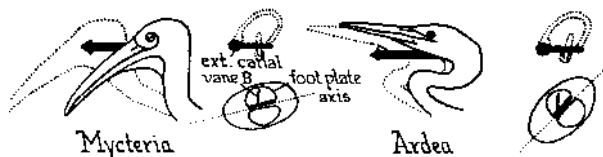


Figure 6. VANE B IN NORMAL POSITION. Illustrates independent orientation in different species of (a) external semicircular canal; (b) axis of the auditory meatus and the foot plate; (c) vane B (vane A is lacking) . In such non-passerines, vane B orients vertically, transverse to forward thrusting movements.

normal thrusting movements of the head in its rest attitude. The contrast between the wood ibis (*Mycteria*) and great blue heron (*Ardea*) in the figure is made to point up these differences. The normal attitudes of the head in these two are shown to be those in which the external canal is horizontal in each case—with the bill directed downward in the ibis and slightly upward in the heron. In the thrusting-retracting movements of the head in walking, these very different attitudes are in each case maintained ; nevertheless vane B has rotated in each so as to be vertical or transverse to these movements and to the thrusting head movements of feeding ! This requires a vastly different amount of rotation of the vanes in the two species, since the axis of the foot plate—always orienting itself with the axis of the tympanic cavity—is very different in each. Again, here is evidence that there is selection on the vane to orient transverse to the direction of air impacts in species whose normal head attitudes in resting and feeding are very different from each other.

It seems unnecessary to multiply examples. This is the rule, based on a vast number of cases of independent vane orientation in species with the foot plate in dissimilar axes. A rather thorough survey of the entire class *Aves*, in which members of all families were carefully sampled, suggests that the orientation of the canals, of the tympanic cavity and of the vanes all vary independently in response to different selective factors. Thus, the external semicircular canal must always be horizontal, no matter how changes in feeding, seeing, etc. may rotate the rest of the skull. *The vanes appear to orient independently athwart the direction of the most characteristic thrusting movements of the head.*

Negative Vane Functions.—The suggested motion sense may co-ordinate head-movements with those of the eyes in feeding. That head movements in animals with lateral vision are closely-associated with food-getting has long been suspected. Grinnell (1921) invented the term "rapid peering" for this behavior and it seems to be practiced by the majority of ground-feeding birds. In starlings, grackles, pheasants and pigeons, the constant thrust and retraction of the head when foraging is well-known, and impacts in the middle ear are a virtual certainty, since vane B is oriented transverse to the

movement. But, when a pheasant that has been foraging in this manner breaks into a run, its head ceases bobbing and is held quite stationary in space. Ducks and geese have vane B similarly-oriented and, when herded about in flocks on dry land, do not practice rapid peering. The head is held quite even by all flock members which turn in unison with the heads always directed the same way, just as in flight. The lack of air impacts on vane B in this case would equally well inform the birds of the lack of acceleration change in their heads.

But the extreme example of this negative function of the vanes is seen in the movie-strip analysis of food-scratching in the fox sparrow (*Passerella iliaca*) in fig. 7. It was, in fact,

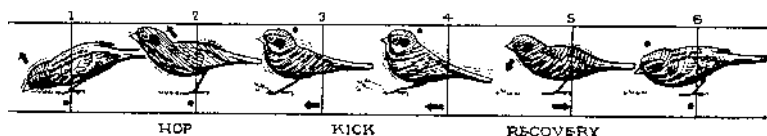


Figure 7. NEGATIVE VANE FUNCTIONS. Analysis of film strip of the fox sparrow (*Passerella iliaca*), food-scratching. The vertical lines, numbered 1-6, represent the same point in space throughout; arrow indicates movement; dot, non-movement. The kick is made with both feet at once, through a great contortion of the body, while the head remains fixed in space.

this remarkable feat of balance that first led me to suspect the presence of a motion sense based on the inertia of air. In my survey of the passerine skull (Beecher, 1953) I could not explain adaptively the inflation of the occipital wing in emberizine finches. The condition results, as shown for *Pipilo* in fig. 3, in a very large external ear, bounded by thin bone (in *Gallus* the much smaller one is bounded by cartilage). At the same time the air vanes, A, B and C, have reached extreme development and the air sinuses of the middle ear region are also maximal in size. This ear seems to be the end-product of a long evolution—extremely sensitive to internal and external air impacts. Not only would any particular head thrust seemingly produce air impacts on a particular vane inside the tympanic cavity but it would also produce an effect in the same direction on the drum externally. This follows because the air inside the bony conch of the outer ear is not only maximal in mass but has access to the outside by only a relatively narrow meatus. In the inflation of the oc-

cipital wing, we may be seeing the last step in this evolution, in which added sensitivity to air impacts is achieved by momentary trapping of air in the outer ear.

The scratching of such emberizine finches as the towhee (*Pipilo*) or the fox sparrow (*Passerella*) strikes me as being co-ordinated by the vanes, but not because of air impacts on them. Quite the reverse ; it may be a negative vane function. This remarkable scratching feat involves a spasmodic thrusting forward, simultaneously, of both feet, then returning them under the body in one-sixth of a second. As seen in the analysis of the movie strip in *fig. 7*, the head maintains a perfectly fixed position in space during the most violent activity of the body. This is the common feeding method of these birds, performed constantly, by which litter is thrown in front of them for examination. I believe that the head *must* be fixed in space at the moment of thrusting forward of the feet to maintain equilibrium, easily thrown off if one hind claw encounters greater resistance in the litter. In this instant, lack of air impacts in the ear may report the static position of the head.

The inflation of the occipital wing, elongation of the hind claw, and the trait of scratching, are found correlated in most of the American emberizine finches, a large number of species. For those not familiar with this group I will mention the white-throated, white-crowned and Harris sparrows (*Zonotrichia*) ; song, swamp and Lincoln sparrows (*Melospiza*) ; vesper sparrow (*Pooecetes*) ; savanna sparrow (*Passerculus*) ; tree sparrow (*Spizella arborea*) ; rock sparrow (*Aimophila*) ; desert and sage sparrows (*Amphispiza*) ; fox sparrow (*Passerella*) ; towhee (*Pipilo*) ; junco (*Junco*) ; and the neotropical finch, *Atlapetes*. A few emberizines with less inflation of the occipital wing and shorter hind claw do not seem to scratch. Mrs. Nice, in addition to publishing much of the above information (1943: 42) , observed that the field sparrow (*Spizella pusilla*) apparently does not do so. She kindly checked this with Drs. G. M. Sutton and L. H. Walkinshaw, as well as Mrs. Amelia Laskey, who agree that neither chipping nor clay-colored sparrows (*S. passerina* and *pallida*) scratch. These are smaller species and the inflated occipital wing and claws are smaller, to the point of being delicate. Possibly, the

scratching reflex has ceased to be useful in the grassland habitat they originally preferred. Something of the sort is suggested in the snow buntings (*Plectrophenax*) and long-spurs (*Calcarius*), which have the inflated occipital wing but the long hind claw is convergently re-directed to a lark adaptation. These species walk in a creeping fashion as they "graze" on abundant ground seeds. They do not hop as other emberizines do.

Finally, there is a small group of primitive American emberizines entirely lacking the inflation of the occipital wing and the development of the hind claw—the true buntings (*Passerina*)—and these never scratch. This is also true for the closely-related finches of south temperate America, represented by *Poospiza*, and for the Old World emberizine finches. No scratching has been noted among the latter either (personal communication of H. E. Wolters to Mrs. Nice) . No member of the several other large finch groups (generally called subfamilies) , numbering hundreds of species, has the inflation of the ear and large hind claw, combined with this peculiar forage-scratching.

The same kind of correlations of activity increase with increase in vane adaptation and in the air mass acting on the vanes—will now be traced in mammals.

AIR VANE MODIFICATIONS OF THE EAR IN MAMMALS

The familiar elbow arrangement of the auditory ossicles of mammals is quite different from the more direct arrangement in birds of a rod-like columella, surmounted by a cartilaginous extracolumella contacting the drum. The drum, too, is different, being an inverted cone in mammals when viewed through the external auditory meatus, whereas in birds it projects outward. It is, thus, doubly significant that the orientation of the vanes of the malleus in this entirely different ear plan is transverse to air currents from tympanic and mastoid sinuses (bullae) , that would be set up by the normal movements of the particular species studied. Here is, seemingly, a convergent arrangement in a different vertebrate class for measuring the direction and force of momentary air impacts.

Observations on Ricochetal Rodents — Heteromyidae. — Starting, once again, with observed behavior, this section seeks to establish valid correlations of peculiar structure with

observed activity in terms of the postulated motion sense. The appended excerpts from the literature point up the high activity of pocket mice (*Perognathus*) and kangaroo rats (*Dipodomys*) and their need while jumping with the hind feet at night for a motion sense additional to vision. Nelson (1918) has given us some vivid pictures of the behavior of these animals. Speaking of *Perognathus hispidus* and *flavus* (p. 396 ff.) , he says :

"The first to reach the food would fiercely charge the next comer and always try to leap upon his back, at the same time delivering a vicious downward kick with its strong hind feet . . . Amazingly quick in movements, they would leap now forward, now sidewise, now straight up a foot or more in the air, with almost equal celerity."

He noted the same sort of activity for one of the smaller species of *Dipodomys* (p. 400 ff.) . The primary objective is to leap on the back of the opponent. Facing each other, they leap about, sparring for an opening, then kick with the hind feet like gamecocks. Bailey (1931: 250) mentions a fight between two specimens of *D. spectabilis*:

"In the night they were heard squeaking in angry tones, and turning on the flashlight the writer saw the two largest animals locked in a fierce struggle on the floor. Each had a firm grip on the other, and they were using their hind feet in furious kicks and jabs and tears. Neither made any vocal sound, but the thumping and tearing of the long sharp toenails could be heard, as flat on their sides they fought like bulldogs. . . . Next morning . . . the newcomer was found in its nest box . . . its hips paralyzed. . . The skin was punctured and torn over the back and hips and the skin of the whole back was like a sieve where the spike-like toenails had been driven through it and into the flesh below. This was apparently the main cause of death. . ."

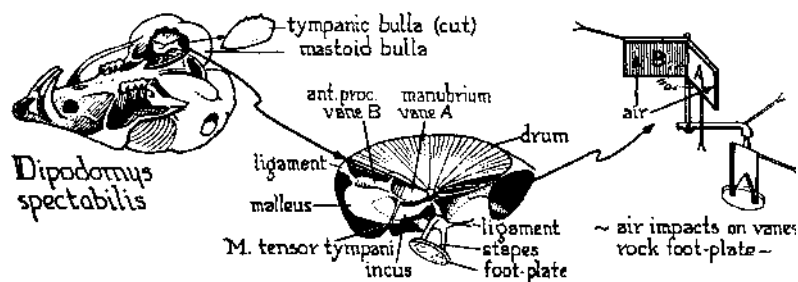
He agrees with Nelson that, in the usual method of fighting, the animals face each other, leaping high in the air and attempting to strike each other downward with the hind feet. If one became tired or turned to run the stabbing blows from the sharp, spike-like toenails of his adversary could be fatal. These blows are delivered with amazing speed and accuracy. Bailey states that several times on reaching his hand into the

nest box he touched a nose "only to be met on the tip of a finger by a sharp stab of the toenails shot under the body and forward with surprising force and accuracy." Elsewhere he notes that the skin was torn off half the body of an individual of *D. merriami* by a single stroke of the hind foot of the larger *D. spectabilis*. I was impressed from the start—knowing that *Dipodomys* has a vast air sinus system in the bullae—with the similarity between the mid-air downward kicks of this rodent and the scratching of the emberizine finches. Analysis of motion picture "kicking matches" between kangaroo rats, show the kicks often delivered in one-tenth of a second, with the body virtually stationary in mid-air. The eyes are usually closed for protection !

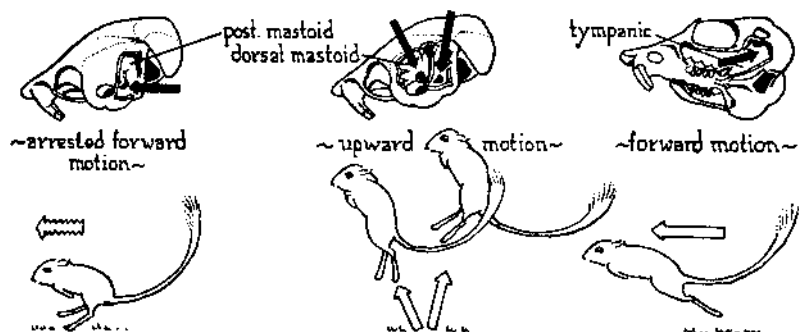
Bartholomew and Cary (1954) claim the pocket mice (*Perognathus*), though leaping as much as two feet in height, always alight on the front feet. Their habits apparently pre-adapted them for bipedalism and ricochetal locomotion. Bartholomew and Caswell (1951) show stop-action photos of ricochetal kangaroo rats, turning in mid-air, always in perfect balance control, illustrating this incredible adaptation.

Air Vane Modifications of the Malleus—Dipodomys.—With the above picture of activity before us, we now attempt to interpret the ear in a typical example of these ricochetal rodents of the American southwest, *Dipodomys spectabilis*. Fig. 8 illustrates the arrangement of the ossicles as seen inside the middle ear through a break in the thin bony wall of the tympanic bulla. The expanded, blade-like *manubrium* of the *malleus* is labeled vane A, the anterior process, vane B. The diagrammatic arrangement of these vanes and the other ossicles as represented to the right, emphasizes that they are, in the same sense as their functional analogues in birds, lightly suspended by ligaments running in all directions to the walls of the tympanic cavity. For this reason, the ossicles are not only sensitive to the sound waves striking the outer surface of the drum (which they propagate to the foot plate) but also, on account of the vane-like expansions of the processes of the malleus, to momentary air impacts within the middle ear, arising from accelerations.

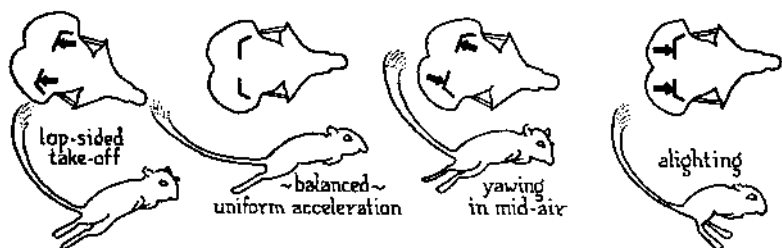
The peculiar, saddle-shaped joint between the head of the malleus and the body of the incus seems capable of movement



AIR VANE MODIFICATIONS OF THE MALLEUS



AIR MOVEMENTS IN THE THREE SINUSES



AIR IMPACTS ON VANES IN FORWARD MOTION

Figure 8. FUNCTION OF AIR VANES IN THE MIDDLE EAR OF MAMMALS.

only in a plane perpendicular to the foot plate of the stapes. Air impacts on vanes A and B, due to movement of the animal, should largely result in movement of the malleus and incur in the plane parallel with the foot plate. Assuming this is true, an impact on vane A should carry a thrust to the joint

between the articular process of the incus and the head of the stapes. As a result, the foot plate should rock downward in the fenestra ovale on the side opposite the air impact and in the axis of the thrust. An impact on vane B should rock the foot plate downward on the side opposite the impact and in the axis in which the air moved. This is exactly the way the more simplified columellar vanes in the bird should rock the foot plate in response to air impacts—on the side opposite air movement and in its axis.

Whether or not one accepts Helmholtz's (1896) ratchet-action explanation when the malleus and incus respond to sound, it seems likely that the two will behave as though ankylosed (Frey, 1911) when responding to air impacts on vanes A and B. In short, they will convey the thrust as a single, fused element. The reaction to an air impact will be much different from that in propagating a sound vibration from the drum. As such it might theoretically be interpreted by the papilla basilaris in the cochlea as a specific movement of the head or of the whole animal.

Air Movements in the Three Sinuses—Dipodomys.—As seen in *fig. 8*, the position of the air sinuses with regard to the vanes of the malleus, in the extreme development noted in *Dipodomys*, is rather convincing of the action of air on the vanes. Two *mastoid bullae*, *dorsal* and *posterior*, occupy the entire region of the skull dorsal and posterior to the middle ear and a *tympanic bulla* occupies nearly the entire ventral part of the skull adjacent to the middle ear. The diagrammatic figure shows how each of these three sinuses opens by a narrow aperture on the auditory ossicles and would thus serve to funnel air to the vanes. In life the tonic contraction of *M. tensor tympani* probably still further narrows this aperture by drawing in the drum. The three bullae are separated by two thin, bony partitions and are buttressed inside by partial bony septa—all in planes converging on the ossicles. There is, therefore, no obstruction whatever to air flow in the direction of the vanes—in fact the entire structure suggests the concentration of a relatively large mass of air by funneling it through a narrow opening (cf. *fig. 2*). The result would be both stronger impact on the vanes and high selectivity of direction.

An attempt is made in *fig. 8* to show the manner in which this arrangement of the air sinuses may function. On the left a kangaroo rat is shown completing a jump. As it alights, and before it takes off again, a momentary deceleration is assumed. The air in the posterior mastoid sinus, due to its inertia, continues in the forward direction at the former acceleration and strikes the posterior surface of vane A, informing the animal of the amount of deceleration. This is supposedly important in achieving the proper body balance for launching on the succeeding jump.

In the second diagram an animal is seen leaping upward. Air is represented as remaining behind in these movements, producing an apparent downward thrust to the vanes in the funnel of either of the two mastoid sinuses, depending on direction of upward jump. In the third diagram the animal is represented as beginning a jump. Air, remaining behind in the ventral or tympanic sinus, would rush posteriorly to strike the vanes. It may also apparently rush upward when the animal descends against its inertia. Thus, in these highly evolved ricochetors, air for impact on the vanes is available in each of the surrounding bullae.

Air Impacts on the Vanes in Forward Motion—Dipodomys. — Recalling that the inertia of air can cause it to have this impact effect only so long as the acceleration is changing, let us attempt to analyze the ricochet of one of these animals. We will suppose that it has alighted somewhat lop-sided and is consequently taking off that way. In the left-hand diagram, showing the dorsal view of the skull, the backward air impact due to forward motion is stronger on vanes A and B of the side toward which the body is turning. It is likely that the long, bushy tail can be employed to correct this and the second diagram shows the animal on its true course in mid-air. The skull shows no air impacts on the vanes now ; the acceleration is assumed to have become uniform and the air has equalized its pressure.

In the third diagram, however, it is assumed that over-compensation by the tail has caused the animal to yaw in mid-air, as a result of which a very slight acceleration on one side, with very slight deceleration on the other, might occur. The fourth diagram pictures it as landing evenly with

equal impact of air on the vanes of both sides from the rear, due to the deceleration.

Drum Effect in Ascent and Descent—Dipodomys.—The foregoing figure gives an approximate idea of the orientation of these vanes when viewed from the dorsal angle. Fig. 9 shows their relationships when viewed from the posterior angle. The tympanic ring—the bony border to which the drum is attached—is seen to be oriented at about 45° to the sagittal plane or about 90° to its mate of the opposite side. As a result, the bony outer ear cavity (indicated in black) is quite large with a relatively small meatus or opening. This is similar to the inflation of the bony outer ear of emberizine finches and we must also assume for these mammals, as we did for the birds, air impacts on the outer surface of the drum. Due, again, to its inertia, air thus trapped in a confined space will act as though closed off from the outside. In balanced ascent there will further be, as noted in figure 8, an impact of air from the sinuses on the vanes, but also on the inner surface of the drum itself, against which the vanes trap it. This will be equal on both sides. But in unbalanced descent, the air trapped in the outer ear is seen in figure 9 to have a more

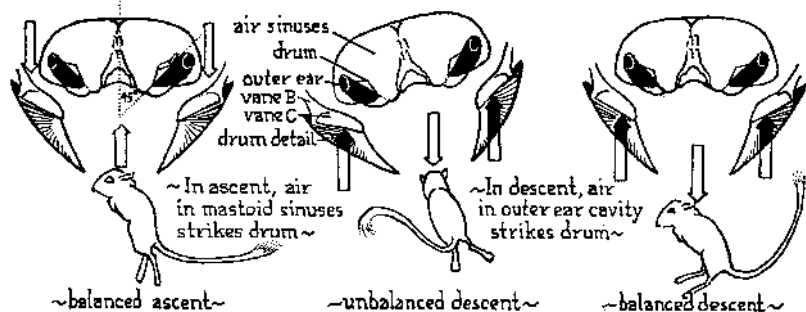


Figure 9. DRUM EFFECT IN ASCENT AND DESCENT.

direct impact on the down-canted side and much less on the other, perhaps reflexly warning the animal. In balanced descent, this pressure should be equal on the outer surface of both drums. For the various other directions of motion, the air impact will be on one or another quadrant of the drum surface, reinforcing the impacts on the vanes inside the middle ear.

Evolution of the Air Sinuses in the Heteromyidae.—It seems clear that the large tympanic and mastoid bullae in *Dipodomys* are an adaptation for the increase in air mass to act on the air vanes of the middle ear. The division of these bullae into dorsal and posterior mastoid and tympanic sinuses, separated by thin, bony partitions, results in three air funnels directed at the air vanes of the malleus. In *Dipodomys*, and still more so in *Microdipodops*, I believe we are seeing the end product of selection pressure for a motion sense utilizing air in the rodent family *Heteromyidae*. It may be of interest to examine some of the still-existent stages of this evolution as probably represented in other genera of the family.

If we examine the skull of a generalized heteromyid rodent like *Liomys irroratus*, Howell (1932: 492) correctly observes that we will find a much poorer development of the bullae and of the bony external ear lying outside the drum. This is especially evident in the mastoid bullae as shown in *fig. 10* where

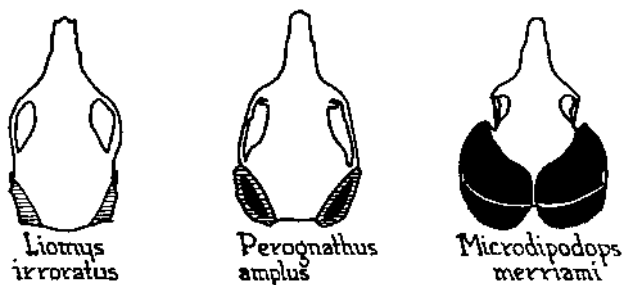


Figure 10. INCREASE IN AIR CAPACITY OF THE MASTOID BULLAE—HETEROMYIDAE. The cancellous bony structure, indicated by hatching, in *Liomys irroratus* is being replaced by air sinus, indicated by black, in *Perognathus amplus*. The enormous air sinus bullae of *Microdipodops merriami* are the end point of this evolutionary trend.

this species has these bullae (hatched area) small and filled with finely cancellous bone. The silky pocket mouse, *Perognathus amplus*, shows higher development the bullae are larger and a central air sinus (black area) has appeared. The culmination is seen in *Microdipodops merriami* where the bullae have reached enormous size with division into dorsal and posterior chambers and no remaining sign of cancellous structure.

In this series no important differences are noted in develop-

ment of the vanes of the malleus. In fact all rodents appear to have the vanes. Once again, what has happened in perfecting the ricochet habit, is that the air mass acting on these vanes has been increased, raising the sensing mechanism to a more effective level.

Convergent Evolution of the Motion Sense in Other Ricochet Mammals.—The simultaneous evolution, convergently, of this precise pattern in several other families of saltatorial or ricochet rodents as well as the family of elephant shrews and the family of marsupial mice, adds support to the hypothesis of the air vanes. It is all the more convincing that these families, so far apart on the phylogenetic tree, have convergently achieved the same end result by rather different evolutionary development.

The Jerboas—Dipodidae.—Many authors have written of the almost birdlike appearance of an undulating horde of leaping jerboas, flushed in car lights at night on the desert, or moving by day too fast for the eye to follow. Howell found the tympanic bulla in Old World jerboas far larger than in any heteromyid rodent. The mastoid bulla, at first very small in *Allactaga*, increases greatly in *Dipus* and reaches full development in *Scirtopoda*. In *Salpingotus* it apparently attains higher inflation than that in *Microdipodops*.

Since they are in an entirely different suborder of the Rodentia from the American kangaroo rats, one quite expectedly notes differences in the Dipodidae. The manubrium of the malleus is even more vane-like than in *Dipodomys* but the anterior process, found in the latter in nearly perpendicular contact with the drum, is oriented horizontally or parallel with the drum in Dipodidae. In *Allactaga*, this horizontal process comes off the side of the rounded head of the malleus, anterior to the manubrium, but in *Dipus* (fig. 11) the rounded

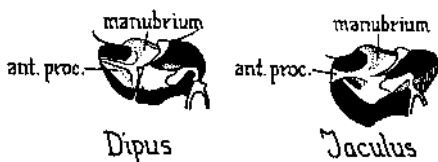
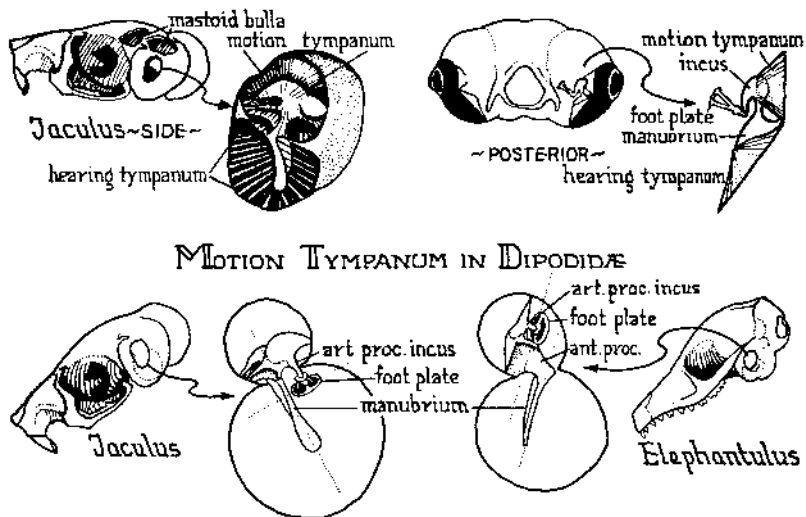


Figure 11. AIR VANE MODIFICATIONS OF THE MALLEUS. Convergent modifications in the jerboas (Dipodidae) for comparison with kangaroo rat (Heteromyidae) in fig. 8.

head appears to have been adaptively eliminated, and little more remains than the long, horizontal anterior process with a new vertical vane attached. This modifies vane B, concerned in *Dipodomys* with air impacts outward (see yawing, fig. 8) but an interesting new structure takes its place. Howell (1932: 499) has called attention to the circular vacuity dorsal to the drum in *Dipus* and *Sciropoda*, across which is stretched a membrane "very comparable to a tympanic membrane." I see no reason for not considering it a part of the tympanic membrane since, in specimens of *Jaculus* I examined (fig. 12), it is continuous with it. I am convinced that it is a part



FORWARD-ROTATION OF MANUBRIUM IN ELEPHANTULUS

Figure 12. CONVERGENCE IN THE EAR OF THE JERBOA AND ELEPHANT SHREW. The ricochetal locomotion may have resulted in great similarity of the ear in these divergent phylogenetic stocks. Compare also with kangaroo rats in fig. 8.

of the drum concerned primarily with motion (though this does not exclude it from a hearing function also), and I propose to call it a motion tympanum. As seen in the extreme right of the figure, this accessory tympanum is deeply concave, investing the malleus and incus in such a way as to move them, in response to air impacts from the mastoid sinus downward and outward and, from the tympanic sinus,

ward and outward. Possibly even more important would be air impacts funneled in by the pinnae (to which this "motion tympanum" is immediately accessible) , when the animal is in a mid-air ricochet. Mellen (1931) compares this functional behavior to bird flight.

This tympanum seems to be an adaptation for making more effective use of air where the air sinuses are not highly developed. The mastoid sinuses are far from maximal in *Dipus* and this is likewise true in the American genera, *Zapus* and *Napeozapus* (the jumping mice) , which have the motion tympanum and are excellent ricochetal jumpers.

The Gerbils—Cricetidae.—The Old World gerbils are most like the jerboas in the arrangement of both air vanes and air sinuses, but still exhibit the differences to be expected in view of their separate origins. The most highly ricochetal forms like *Gerbillus* have the motion tympanum well-developed, in correlation with much inflated mastoid bullae, to supply the dorsal air mass acting downward and forward upon it. Less highly-evolved forms like *Tatera* and *Taterillus* lack the motion tympanum, on the other hand, and the mastoid bullae are small. The manubrium of the malleus is most similar to that found in dipodids but the anterior process has expanded more completely as a vane (with corresponding reduction of the boss-like head) than in any other rodent. It even resembles the development seen in the Carnivora.

Hatt (1932: 624) mentions Australian and Madagascan genera in Cricetidae and also Muridae that probably ricochet and no doubt there are still others.

Cape Jumping Hare—Pedetidae.—This large African rodent, represented by the single species, *Pedetes caffer*, shows an arrangement that could be called a rather clumsy version of that in Dipodidae. The motion tympanum is lacking but the mastoid bullae are well-developed. The tympanic ring to which the drum is attached is more nearly vertical than in the other families and, although the bony external ear is, therefore, less spacious, Pocock (1922) believes the pinna capable of shutting off the meatus. The contained air, thus more effectively trapped, could more efficiently act on the outer surface of the drum.

The Elephant Shrews—Macroscelididae.—The convergent

occurrence of the supposed motion tympanum in the African elephant shrews—still another group of small mammals that has embraced the ricochetral mode of locomotion—further bolsters the view that it is related to that locomotion. Here (*fig. 12*) there is even greater tendency to reduce the bony vanes of the malleus in favor of this more responsive membrane vane. The development of the air sinuses of the bullae is fully comparable in *Macroscelides* with that in the most highly evolved heteromyid and dipodid rodents, though *Elephantulus* has the mastoid bullae much less developed.

Obviously, we should again expect differences in groups as distantly related as the shrews and rodents (Keen and Grobelaar, 1941). A rather striking difference is seen between Dipodidae and Macroscelididae in the different orientation of the manubrium on the drum. Unlike all the ricochetral rodents, which have the articular process of the incus parallel to the manubrium, the elephant shrews rotate it so that it is in *Macroscelides* at about 45° and in *Elephantulus*, about 90° to the manubrium (*fig. 12*). In this change of relationships it is the manubrium which shifts its relation to the rest of the ear and skull most. Since *Macroscelides* is probably more highly specialized with its expanded mastoid bullae, it may be permissible to think that it is approaching the condition in the ricochetral rodents in which the articular process of the incus will be parallel to the manubrium. If not, I am unable to offer an adaptive explanation for the position of the manubrium on the drum, since these animals, judging from the orientation of the external semicircular canal, normally hold the head not much differently from the ricochetral rodents, especially *Dipus* or *Jaculus*.

The net result is that the manubrium, viewed against the drum from the external opening of the ear, points forward as much as 40° from vertical in *Elephantulus*, whereas the ricochetral rodents, in general, have it pointing backwards about 45° . Another difference is found in the *M. tensor tympani*. This muscle, whose function appears to be the drawing of the drum farther into the tympanic cavity, inserts midway on the manubrium vane in all rodents but at the base of the manubrium in the elephant shrews.

These differences are phylogenetic reminders in the ossicles

that the origins of rodents and shrews are different. They render the similarities, convergently arising with the ricochet method of locomotion, doubly impressive and significant.

The Marsupial Mice—Dasyuridae.----If convergence in the functional elements of the supposed motion sense between shrews and rodents is surprising, the occurrence of the same pattern in this family of Australian marsupials (a different subclass of mammals) is even more noteworthy. The genera *Antechinus* and *Sminthopsis* are ricochet marsupial "rodents" which (aside from an enormously heavy tympanic ring characteristic of many marsupials) closely resemble *Elephantulus* in the arrangement of the vanes and bullae. They are, therefore, not greatly different from Dipodidae-- with motion tympanum fairly well-developed, though the arrangement of manubrium and foot plate in parallel axes makes the resemblance closer to the jumping shrews.

The Kangaroos—Macropodidae.—The Australian kangaroo is not considered ricochet in the sense of all the foregoing because its leaps are relatively short for its size and because it does not experience anything like the acceleration changes of the small, ricochet mammals. Keen and Grobbelaar (1941) have observed that kangaroos possess no tympanic bullae. However, the middle ear is quite large, as is the drum. There is a rudimentary motion tympanum and the malleus is very similar in development to that of the marsupial mice, its orientation on the drum being likewise as in the marsupial mice. Though the presence of the motion tympanum might make up for the lack of inflated bullae by permitting direct air impacts on the ossicles from the pinnae, this is plainly a less-evolved system. However, unlike the others, kangaroos are diurnal. Vision may play a role.

Significance of the Convergence.—We see, therefore, that there has been a remarkable convergence of small mammals of vastly different phylogenetic origin in the desert areas of the world. In general these animals show very well all the characteristic features of their respective orders and families. Only in two regions of the body do they resemble each other more than they do their true relatives. The tail and hind appendages have elongated in adaptation to the bipedal locomotion possessed by all and there has been a very similar

development of air sinuses (bullae) , vanes and/or the peculiar motion tympanum of the ear. In my opinion it is extremely unlikely that nearly perfect correlation between the ricochet al locomotion and the special development of the ear in seven or eight phylogenetically-distinct stocks could occur without the locomotion and the ear being functionally related to each other. This seems to be strong evidence for an accessory motion sense in the middle ear, based on the accelerations of trapped air, due to its quality of inertia.

Other Views.—In my opinion this correlation with locomotion does not eliminate other theories about the function of the inflated bullae in these mammals. In one form or another these theories all express the idea that these air chambers permit the animal to hear better (Howell, 1932: 385 ; Webster, 1966) . Keen and Grobbelaar (1941: 329) even express the extreme view that the auditory ossicles in many mammals are merely vestigial structures and that hearing is accomplished directly through the thin bony walls of the tympanic bulla and the cochlea.

Hatt (1932) believes that the "inflation of these bullae is not in itself a response to upright posture or ricochet al progress, for it is found in varying degrees among many desert-living, strictly quadrupedal mammals." It should be remembered, however, that these mammals are virtually all nocturnal, because of the desert heat by day, and highly saltatorial. As swift runners in a very open habitat they may need special development of the motion sense since their eyes may not function sufficiently well at night. This is simply all the more so for the ricochet al forms. Howell (1932: 386) has observed of *Dipodomys*:

"When panic increases the length of the leap to the neighborhood of six feet the speed of the animal would seem to exceed its control . . . it is then likely to make a rather poor, unbalanced landing, and . . . before full recovery has taken place a powerful kick by the hind feet will often send the animal hurtling through the air once more in a more or less lopsided fashion. If in an especial hurry it may thus fail to plan its course with proper foresight and occasionally will land amid the dense twigs of a small shrub in anything but a tactical position."

Such a nocturnal animal might need a special motion sense. In alighting and immediately taking off again, it must know its accelerations and decelerations precisely and automatically in order to maintain balance.

The Motion Sense in Other Rodents.—The vanes and air sinuses are not the exclusive possession of the ricochetal rodents. They are common to all rodents. I have simply pointed out that, as activity increases with ricochetal locomotion, there tends to be an increase in size of the air sinuses—or else the motion tympanum evolves to make more effective use of the available air mass. In *Sigmodon* and *Peromyscus* of the rodent family Cricetidae and in *Rattus* of the family Muridae the evolution of a motion tympanum seem to be within each reach, should these genera become ricochetal. The secondary tympanum already exists and is continuous with the hearing tympanum in the same plane—only it does not invest or even contact the ossicles as in ricochetors. Nevertheless, due to the great vane-development of the anterior process of the malleus in *Peromyscus* and *Rattus*, this motion tympanum, however rudimentary, is probably already functional. Air impacts on it via the large pinna, due to the saltatory (though not bipedal) locomotion of these rodents, could be transferred to the anterior process—just underlying it in the same plane—by means of the pneumatic cushion of air, momentarily caught between these two flat surfaces. This would be most efficient in *Peromyscus* because the surfaces are closer together. In *Sigmodon* the anterior process is less well-developed. These relationships seem to be in good agreement with their comparative activity.

Microtus has good bullae and well developed vanes, though the anterior process is not as well-developed as above and the bullae show some of the cancellous structure seen in the pocket gophers (Geomyidae) and in the less active heteromyids. This is to be expected since these short-legged mice lack the jumping proficiency of *Peromyscus*—and also lack entirely the fenestra for the motion tympanum.

Among the squirrels (Sciuridae) fairly good vane and bulla development is found, though their rapid accelerations and decelerations, while more familiar, are no match for those attained in small mice. As a matter of fact the malleus in these

rodents is somewhat more like that in carnivores and ungulates. All have the tympanic bulla well-inflated. But the flying squirrels, *Glaucomys* and *Petaurista* have a fair mastoid bulla.

The peculiarity of the malleus of the rabbits and hares (Leporidae) supports the view that they are a separate order—but there is still close conformance as far as the vane development and orientation is concerned. The tympanic bulla is quite large and a secondary or motion tympanum is present, in which the relationship to the anterior process of the malleus is as in *Peromyscus*. As in the *Pedetidae* the tympanic ring is nearly vertical but the relatively narrow outer ear is directed upward. Possibly air impacts are thrust downward to the motion tympanum by the upward jumps of the animal and lopsided jumps could be reported by difference in impacts on the drums of either side.

In all the above a gradient of vane and sinus development is apparent. With minor exceptions, it is greatest in ricochetors, intermediate in jumpers, least in slower forms

The Motion Sense in Carnivores and Ungulates.—The ricochetal mammals were chosen as an example of extreme development of the proposed accessory motion sense, but it is plain that the apparatus could function in almost all remaining mammalian orders. As in the ricochetors, it is the malleus in the remaining groups that exhibits vane-modifications, and the most common pattern of development is that seen in the two large, remotely-related groups—the carnivores and ungulates. This pattern, as seen in the malleus of *Ursus* (fig. 13), shows the expansion of the manubrium into a flattened vane in contact with the drum, and the expansion of the anterior process as another vane, often very delicate and light in construction. Comparison of this malleus with that of *Odocoileus*, *Aepyceros* and *Connochaetes*, the ungulates shown in the same figure, with *Mustela* in fig. 14, *Fennecus* in fig. 15 and *Felis* in fig. 16, shows the similarity in the development of these vanes. This similarity extends to the orientation of the bony tympanic ring in the skull and to the orientation of the malleus on the drum.

Observations on Carnivores and Ungulates.—Gregory (1937) likened the mammalian vertebral column to a suspension

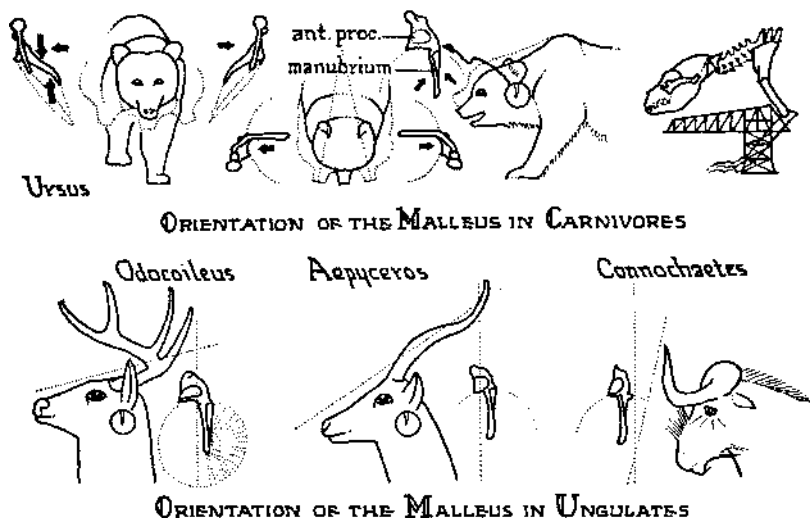


Figure 13. ORIENTATION OF THE MALLEUS IN CARNIVORES AND UNGULATES. The malleus in the bear (*Ursus*), and in deer (*Odocoileus*), impalla (*Aepyceros*), and gnu (*Connochaetes*), has the vanes similarly developed and is similarly oriented on the tympanum. This orientation may permit detection of air impacts in all three planes of space.

bridge and Slijper (1946) develops the idea quite thoroughly. Howell (1944) makes an important addition, in my opinion, in suggesting that the skeleton, unlike the bridge, encounters stresses just as strong from lateral or upward directions, as from the downward direction of gravity, and is not solid but articulated. All three view the head as suspended from the anterior pier (dorsal spines of the thoracic vertebrae) by a muscular sling. In my figure 13, I liken this arrangement to

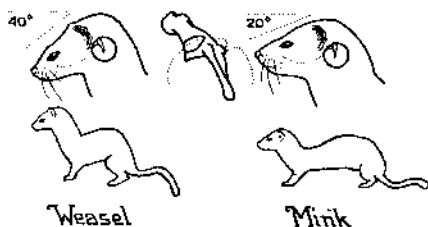


Figure 14. ORIENTATION OF THE MALLEUS IN SMALL CARNIVORES. The malleus and its orientation in the weasel (*Mustela noveboracensis*) and mink (*M. vison*) is similar to that of larger carnivores and ungulates.

a giant crane but it is even better in the large mammals, in that the boom representing the neck may be raised and lowered, as well as swung from side to side. This is important, because the carnivores and ungulates characteristically exhibit bobbing movements of the head in co-ordination with the movements of the appendages in locomotion.

As seen in the bears (Ursidae) and cats (Felidae) , these movements suggest a slack swinging of the head from the muscular sling originating on the dorsal spines of the first thoracic vertebrae. The head of the bear or cat moves freely from side to side or bobs slightly up and down with the easy



Figure 15. ORIENTATION OF THE MALLEUS IN THE DOGS. The malleus in the fennec fox (*Fennecus zerda*) is little modified from the carnivore pattern.

jar of each step. There is in the neck of mammals some suggestion of the S-shape noted for birds, and the origin of these head movements near the thoracic origin of the neck may impart a more thrust-retractional than rotational character—so that the semicircular canals may not adequately report them. This thrust-retraction movement is more obvious in the tearing of food by carnivores.

An important shift in emphasis is thus noted in the larger mammals. Whereas the rodents probably utilize the new motion sense in reporting acceleration changes of the entire body, the larger mammals have the vanes oriented in correlation with the characteristic head movements. These head movements might be co-ordinated with rhythmical movements of the extremities in locomotion by a reflex arc originating in the neck, but may also be connected with vision by a reflex arc

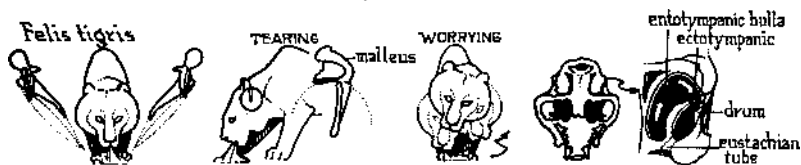


Figure 16. THE MALLEUS AND THE TWO-CHAMBERED BULLA IN CATS. Orientation of the malleus in the tiger (*Felis tigris*) and other cats is a little forward of vertical.

possibly originating in the cochlea.

Orientation of the Malleus in the Bears—Ursidae.—The vanes in the ungulates and carnivores lie approximately transverse to air currents that would be set up by the normal head movements. The aforementioned figures for these groups, like those of the ricochetal mammals, show the heads generally oriented in the normal rest position, in which the external semicircular canal is horizontal. With the head of *Ursus* in this position (*fig. 13*) , the drum is seen in anterior and dorsal views stretched across a tympanic ring, which slants ventromedially in a plane at about 45° to the sagittal plane and, at the same time about 30° posterolaterally. The manubrium of the malleus, in contact with the drum and maintaining its inverted umbo, is oriented nearly vertically in the transverse plane of the skull, while the anterior process is nearly vertical in the sagittal plane (it slants about 10° ventromedially) . The position of the drum itself insures that downward impacts of air inside the tympanic cavity and upward impacts in the outer ear will strike it, effecting movements of the ossicles accordingly. The manubrium is seen from the side in the same figure. Since it slants only slightly posteriorly in its attachment to the dorsal quadrant of the drum, it may trap downward air impacts inside the tympanic cavity against either anterior or posterior quadrants of the drum. Thus, the backward or forward component of this mainly outward movement of the drum and malleus, due to air impacts, would produce a down-rocking of the foot plate on either the anterior or posterior border. It is also evident that, for each up and down movement of the bear's head, there may be an out and in movement of the foot-plate in the fenestra ovale which might be co-ordinated with vision via the papilla basillaris. In correlation with its extreme head-bobbing, the giant panda (*Ailuropoda*) has these vanes very highly developed.

Vertical Position of the Manubrium in Carnivores and Ungulates.—It was stressed in the bears that the manubrium slants only slightly posteriorly when viewed from the side—as one would see it upon looking into the external auditory meatus when the animal has its head in the normal attitude. This position is the most general one noted in mammals,

though some, notably the cats, have it directed somewhat forward of a vertical position on the drum. That there is something fundamental about this position is suggested by the fact that the deer, impalla and gnu have the manubrium in the same nearly vertical orientation on the drum (*fig. 13*) despite the fact that the normal head attitude is different in all three. It is nearly horizontal in the deer (*Odocoileus virginianus*) and its relatives, depressed 45° in the impalla (*Aepyceros melampus*) and other related gazelles and antelopes, and nearly vertical in the white-tailed gnu (*Connochaetes gnou*). This suggests the rotation of the skull with respect to the semicircular canals, as noted in birds, and it will be recalled that in birds, too, the vanes tended to achieve a common orientation in many species, despite vast modifications of the skull.

Just as in birds, this differential rotation is to be noted between rather closely-related species of mammals. In the Mustelidae the weasel (*Mustela noveboracensis*) carries the head with the snout more strongly depressed than the mink (*M. vison*), as evidenced by the semicircular canals (*fig. 14*). The depression from horizontal is about 20° in the latter, 40° in the former. But, in both, the manubrium is precisely transverse to the long axis of the skull. Although the head moves up and down in the looping gait of these little carnivores, the thrusting movements of the head in seizing prey may possibly govern this orientation of the manubrium on the drum. In all carnivores and ungulates it is oriented to report accelerations and decelerations in the forward direction.

The dogs (Canidae) have the normal position of the manubrium as indicated in the fennec fox, *Fennecus zerda*, of Africa (*fig. 15*) and this is equally true for the horse (*Equus*), shown in *fig. 17*. In the latter figure the possible function of the manubrium in trapping air impacts against the anterior or posterior quadrant of the drum is suggested. Thus, the direction of air impacts on the inside of the drum will most often be against the anterior face of the manubrium (indicated by the anterior black arrow) because of the angle at which the animal normally lifts its head in locomotion. This is supported by the fact that the concave face of the manubrium is forward. But the impact may be against

the convex posterior face of the manubrium if the head is oriented more nearly vertical in these bobbing upward movements (as when a horse is reined in). These relationships, along with the co-ordination of head and limb movements, suggest how it may be possible to train a five-gaited horse to go through its gaits in response to the reins. Howell (1944: 219) points out that the order of foot-fall in a gait is regulated by a complex nervous reflex arc. Since this may be initiated in the neck, I do not propose that it is necessarily dependent on air-impacts reaching the vanes—but a sensory awareness of head-movement may be necessary for proper visual compensation.



Figure 17. ORIENTATION OF THE MALLEUS IN THE HORSE. The manubrium is believed to trap air impacts against the anterior or posterior portions of the inner drum surface (indicated by black arrows) as the animal rhythmically lifts its head in normal locomotion.

Function of the Anterior Process in Carnivores and Ungulates.

—It has already been noted for *Ursus* (fig. 13) that the anterior process of the malleus lies nearly vertical in the sagittal plane. It is, thus, nearly transverse to air currents set up inside the tympanic cavity, due to head movements from side to side. It is easy to see that a swinging of the head to the left will produce an air impact on the inner surface of the right anterior process as well as on the drum and manubrium. It will, however, produce a different rocking of the foot plate from that resulting when a downward impact of air on the manubrium and drum follows an up-swinging of the head. In the case of the head-swing above, air strikes the medial surface of the anterior process—but in many carnivores and ungulates the lateral surface appears to be better adapted by its concavity to intercept air movement.

The Two-chambered Tympanic Bulla in Cats (Felidae).—

The locomotion of the cats may be compared with that of bears so far as the head movements are concerned but there is a notable difference between the two in the air sinuses. As

shown at the extreme right in *fig. 16* (section through the tympanic bulla of *Felis domesticus*), there is an entotympanic bulla in addition to the ectotympanic bulla into which the external auditory meatus directly opens. This entotympanic bulla is the larger of the two and communicates with the more lateral ectotympanic bulla by a foramen just posterior to the drum, a situation duplicated in most viverrids. The rounded contours of both chambers suggest an adaptation for getting greater air mass to act anteriorly on the drum and manubrium through this foramen. Thrust-retraction head movements are coupled in cats with side-to-side worrying movements by means of which meat is torn from the prey. Air movements set up within the bullae may possibly act "around the curve" of the bulla wall as indicated by the arrows.

The Motion Sense in Edentates (Edentata).— Although some of the mammals of this order may have clearly undergone loss of activity, the anteaters (Myrmecophagidae) and armadillos (Dasypodidae) are still capable of considerable activity, exhibiting much head swinging in feeding. In agreement they have both the manubrium and anterior process of the malleus rather well-developed and the tympanic bulla (a functional entotympanic occurs in some species) correspondingly so. The sloths (Bradypodidae), on the other hand, seem hardly capable of movements producing air impacts on vanes and the anterior process is largely lost through thickening of the bone. The manubrium is still quite vane-like and it seems likely that reduction would occur but slowly with reduced activity so long as the ear remained functional for hearing. The tremendous increase in mass of the auditory ossicles of the whales, manatees and pinniped carnivores with loss of hearing by air vibration (Doran, 1878) may be a case in point. The ossicles might also function as a motion sense by virtue of their mass and inertia. With their mass they would be more effective than featherweight ossicles designed to utilize the mass and inertia of air in a motion sense, while functioning for hearing as well. However, Webster (1966) explains them in terms of underwater hearing.

Other mammals showing loss of vane character in the malleus with reduction in activity are the Old and New World

porcupines (Hystricidae and Erethizontidae) .

The Motion Sense in the Aard-vark (Tubulidentata) .—The so-called earth pig (*Orycteropus afer*) has excellent development of the anterior process as well as the manubrium. Clark and Sonntag (1926) do not give any detailed notes on feeding functions but my observation of a zoo specimen suggest that the vane development will be found to be associated with head swinging. The middle ear in *Orycteropus* is not enclosed by bone but a fairly large air space is indicated by the tympanic ring.

The Motion Sense in Bats (Chiroptera) .—As in *Orycteropus* the bulla (mainly entotympanic) is incomplete, though a fairly large air sinus is present. Much of the tympanic cavity is occupied by the abnormally large cochlea, probably associated with obstacle avoidance through the hearing of supersonic sounds, emitted by the animal and reflected back by obstacles (Griffin and Galambos, 1941) . The drum is very large in the insectivorous bats (Microchiroptera) , with good development of the manubrium and exceptional development of the anterior process, associated possibly with rapid direction change. The fruit bats (Megachiroptera) , larger and slower, have only the tympanic ring bony, but the vanes are well-developed.

The Motion Sense in Insectivores (Insectivore) .—Very good development of both the manubrium and anterior process of the malleus occurs in the golden mole, *Chrysochloris* (Chrysochloridae) , in the common mole, *Scalopus* (Talpidae) , in the shrew, *Crocidura* (Soricidae) and in the hedgehogs (Erinaceidae) . The bullae are open in the shrews as in bats but ample air space is apparent in all. The drum on its tympanic ring is oriented more nearly horizontal than in any other mammals and I should expect the up-down movement of the head to be most prominent in these forms.

The Motion Sense in Flying Lemurs (Dermoptera) .—The flying lemur of Malaysia (*Galeopithecus volans*) has both vanes well-developed with a good bulla.

The Motion Sense in the Primates .—The primate pattern in the auditory ossicles is already forecast in the tree shrews (Tupaidae) . *Tana* has the manubrium only moderately vane-like, though there is a large drum and bulla—and fairly ob-

vious head-bobbing has been noted in this active little animal. The anterior process is not vane-like. Passing upward through the lemurs and monkeys, we note only a decrease in size of drum and bulla with decrease in activity—and, generally, with larger size of the animal. In the apes and man, both become relatively small. Van der Klaauw (1931) states that the whole bulla is entotympanic in *Tupaia*, probably in all primates having a single chamber.

There are some modifications in the more active species. An active form like the tarsier (*Tarsius*) has a separate entotympanic bulla as in the cats and the drum, which is very large, lies at an angle of 45° to the sagittal plane. In most Primates it is more nearly vertical. The bush baby (*Galago*) jumps about on the ground like the ricochetors and has mastoid as well as tympanic bullae developed as five distinct chambers leading into the tympanic cavity. The manubrium in this form is, correspondingly, the most vane-like I have noted in the order. The lemurs all have good bullae and, generally, large drums—but the manubrium is not vane-like. The nearly vertical position of the drum suggests that unequal air impacts via the pinnae on either side may be helpful in keeping balanced in long jumps, after the fashion of a rudder. Some of the New World monkeys, especially *Cebus* and *Ateles* (Cebidae) show suggestions of the chambered bullae noted in *Galago*. Old World monkeys have the bullae more completely filled with cancellous bone. No great development of the proposed motion sense would be expected since they are diurnal.

Size of bulla and drum, generally, decrease relatively with decrease in activity and larger body size. The reduction is rapid in the anthropoids and in man and may be positively correlated with diurnal feeding, upright habit, forward vision and increased use of the hands in feeding. In man, a thrust and retraction of the head is no longer possible in the sense that we have studied it in other mammals. To say that man completely lacks the new motion sense may be unwarranted, even though he no longer has the problem of making visual compensation for thrusting head movements, but it is certainly greatly reduced.

Negative Vane Functions in Mammals.—In this connection it is interesting that many of the carnivores and ungulates

have gaits in which the head appears to be virtually non-moving relative to the body. These are apparently gaits offering maximum support and equilibrium with least effort (Howell, 1944), in which each foot falls separately in rapid succession or in which diagonal pairs fall alternately. Such gaits are the rack and trot in the horse, for example. The various species of the dog family commonly have such gaits. Just as in the scratching of the emberizine finches, it appears that lack of air impacts on the ear vanes in these gaits could furnish negative reports to the papilla basilaris.

VANE MODIFICATIONS OF THE EAR IN OTHER VERTEBRATES

A cursory survey of the skulls of the remaining vertebrates at first indicates little suggestion of vane-modifications in the middle ear for the interception of air currents. The bony columella or stapes is simple and rod-like in all cases. Anatomical specimens, however, reveal sheet-like membranous and cartilaginous "vaness," connecting the columella to the wall of the tympanic cavity and to the drum.

Recapitulating, it was emphasized that the arrested thrust and retraction of the avian head produced air impacts on the cartilaginous and bony vanes and that this seemed to be the case in many mammal groups. In jumping animals, especially rodents having little head-movement, the acceleration changes of the body as a whole were judged responsible for air impacts in the middle and outer ear. The remaining vertebrates would likewise fall into one of these two categories. Turtles are capable of rapid thrust-retraction movements of the head on the S-shaped neck but lizards, with relatively little neck movement, accelerate and decelerate the entire body rapidly. Both have membranous vanes, securing the columella to the walls of the tympanic cavity and to the drum. The vanes of frogs even bear a resemblance in shape and orientation to those of jumping rodents, though they are not nearly so well-developed and are of cartilage and membrane instead of bone.

VANE MODIFICATIONS OF THE EAR IN LIZARDS

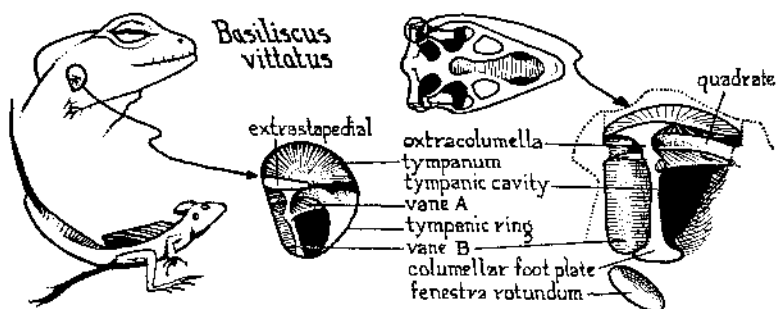
Despite behavior differences among the numerous families of lizards, there emerges—as in birds—a generalized pattern, common to all species having a fully-developed hearing ear. with

sponds to the "normal lacertilian ear" of Smith (1938) . What he calls the "dorsal process" of the extrastapedial supports a membranous vane, running the length of the columella and its cartilaginous extension (extracolumella) —securing it to the dorsal wall of the tympanic cavity. I shall call this vane B, though it is neither homologous nor analogous to that vane in birds or mammals. In bipedal running, some lizards (e.g. *Basiliscus*) hold the head with the snout upturned about 45° so that this vane is nearly horizontal. This is seen by the position of the extrastapedial, visible from the outside in contact with the slightly out-bowed drum (*fig. 18*) . Although this vane may have sufficient downward angle to have some effect in detecting forward-backward impacts, it is ideally oriented for reporting up-down air movements in the tympanic cavity.

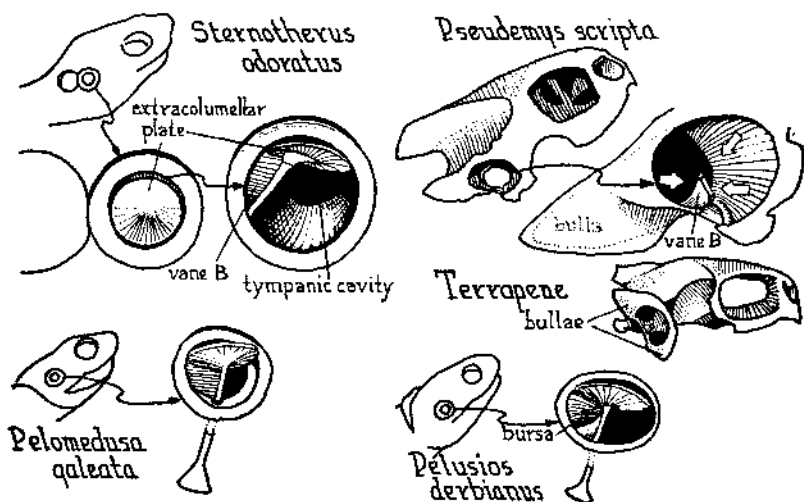
Another vane, extending between Smith's "internal process" and the quadrate, is vertically-oriented in the sagittal plane. This vane A (so-named) may report air impacts from either side, to produce an in-out movement of the foot plate in the fenestra ovale, assisted by impacts on the outer surface of the drum, itself. These two vanes, therefore, constitute something resembling the rudder and stabilizer of an airplane which may be especially important in the bipedal running on the surface of water by *Basiliscus*, as reported by Hallinan (1920) , and more recently and fully, by Snyder (1949) .

Orientation of the Vanes in Lizards.—The orientation of these vanes in the Lacertilia with respect to direction of air impacts depends on the normal position of the head. Howell (1932: 395) has noted in mammals that the canthi or "corners" of the eyes, when lined up horizontally, seem to define the normal attitude of the head. This rule appears to work out in vertebrates, generally, and I have found it in good agreement with the horizontal position, previously noted, of the external semicircular canal. Thus, the orientation of the vanes as rudder and stabilizer in the bipedal basilisk may aid it in maintaining its precarious equilibrium. Perhaps the exposed drum, itself, is able to report forward acceleration and yawing.

On the other hand, the six-lined skink, *Cnemidophorus sexlineatus*, noted for rapid accelerations and decelerations, has these vanes (following the columella) rotated counterclock-



AIR VANES IN LIZARDS ~ Lacertilia



AIR VANES IN TURTLES ~ Chelonia

Figure 18. AIR VANES IN THE MIDDLE EAR OF LIZARDS AND TURTLES.

wise in the skull (viewed from the left) and carries the head a bit less elevated. The net result is that vane B slants downward at an approximate angle of 45° to the backward air impact from forward motion. In this position it might report both forward-backward and up-down air impacts by different rocking of the foot-plate. The vertical vane (A) would report side impacts as in *Basaliscus*, for sideward head-movement is characteristic in all lizard locomotion. This is the rule in other species of this genus as well, though *Cnemidophorus*

murinus and *octolineatus* have the vanes slightly less-developed.

The generalized condition of the columella and its vanes, as outlined for *Cn. sexlineatus* of the family Teiidae, is found in generalized members of other lizard families. In the family Agamidae, *Amphibolurus* and *Calotes* have it. In the family Iguanidae, *Crotophytus collaris*, *Phrynosoma cornutus*, *Uta thalassius* and *Sceloporus undulatus* have it. *Xantusia riversiana* (Xantusiidae) and *Varanus* (Varanidae) also have the pattern, though a little less well-developed in the larger, clumsier *Varanus*. *Gekko* (Gekkonidae) has a very similar arrangement (Smith, 1938) .

Vane Persistence with Adaptive Reduction in Hearing.— Adaptive reduction or degeneration of the hearing ear has taken place in a number of lizards, possibly reflecting disuse in these forms in favor of more complete scaly protection of the posterior head region. However that may be, we find in the family Agamidae as pointed out by Smith (1938) some forms of *Draco* that have the tympanum exposed (*D. everetti*) and others in which it is covered with scales (*D. spilopterus*). Other genera like *Lyriocephalus* and *Ceratophora* have lost the tympanum entirely, its place being covered by the anterior branch of *M. depressor mandibulae*. Such changes certainly indicate reduction of air perception of sound, yet the membranes holding the columella in place could undoubtedly intercept air currents as vanes. Hence we see in Agamidae a persistence of vanes, together with a large available air mass to act on them.

In *Holbrookia*, the only genus of the Iguanidae in which the tympanum has been lost, the columella has degenerated so that its knoblike head is in contact with the posterior surface of the quadrate, the cartilage extracolumella being lost entirely. Nevertheless, the columella is extremely free to move and is attached to a strong membrane lying in the horizontal plane in *H. maculata* and to two membranes in *H. texanus*. The second of these in *H. texanus* should be capable of intercepting forward-backward currents, while the first in both species might intercept up-down currents set up by the jerky raising and lowering of the body mentioned by Smith (1946) . Although the entire extracolumella appears to be missing, this genus seems to have availed itself of the vane B, found

well-developed in *Crotophytes collaris*, and further specialized it.

Reduction of the Vanes with, Reduced Activity.—In the above species, no notable diminution of activity of the lizard has accompanied degeneration of the hearing ear ; hence the persistence of the eustachian openings and membranous vanes with reduction in hearing may add support to their postulated role in reporting motion. A check on this should be provided by consideration of genera that have become slow-moving. I am familiar in the field with the prehensile-tailed skink (*Corucia zebrata*) of the Australian region. It is a slow lizard and has greatly reduced vanes, despite a well-developed tympanum. Burrowing lizards such as *Amphisbaena* (Amphisbaenidae) or *Ophisaurus* (Anguidae) , which have entirely or almost entirely lost the limbs and do not move as rapidly as normal lizard types, prove to have no vanes at all, so far as I can see. Of course both of the latter have lost the tympanum and the hearing ear is quite reduced in all respects.

Significance of the Convergence in Lizards.—What we seem to see in the various lizard families is adaptive convergence of different stocks, based on activity, so far as the ear is concerned. The sensitivity of the membranous vanes and of the tympanum, combined with the large air space in the tympanic cavity and the known celerity of movement, seem to point to one conclusion in the Lacertilia. The air currents set up by the movements will strike the vanes, and rock the columella and its foot plate in a manner distinct from that in propagating sounds. If the vanes served no function, then ligaments, lacking vane-character, could equally well support the columella. However, it is generally noted that, as in the foregoing vertebrates, an increase in vane character and air mass as well as drum size accompanies increase in activity.

VANE MODIFICATIONS OF THE EAR IN TURTLES

Despite general slowness, one might predict air vane characteristics in the middle ear of turtles. The rapidly moving head, which assures them their livelihood, terminates a long, S-shaped neck. Moreover, many turtles have an extreme development of what corresponds to the mammalian auditory bullae, although this development in turtles is in a different bone—the squamosal.

The tympanic cavity is in the quadrate, and the foot plate is generally not visible through the external ear opening, the rod-like columella emerging into the tympanic cavity via a narrow foramen (fig. 18, *Pelomedusa*). As in lizards, it shows no bony vane modifications but spirit specimens reveal a very high vane development in the membranes securing it to the walls of the tympanic cavity. This seems to be all the more significant since hearing, at least by air waves, is extremely limited in turtles. Typically, an extracolumellar plate underlies the tympanum, which is also covered by the head scales. (fig. 18, *Sternotherus*). This plate is connected with the columella by a cartilaginous extracolumella.

The Vane and its Orientation.—The single membrane vane is variable in different species but conforms to a pattern similar to that in typical lizards. This is shown for *Sternotherus odoratus* in fig. 18, a single, unbroken vane B, running the length of the columella and extracolumella, and securing them to the tympanum and to the wall of the tympanic cavity. In all of the turtle figures the extracolumellar plate is tilted back into the tympanic cavity to show its underside. In *Pseudemys scripta*, the plate is removed to show the orientation of the vane, athwart the air mass housed in the bulla. In this position, as shown by arrows in the diagram, it would be most advantageously placed to intercept air movements from every direction, as one might expect in view of the fact that a single vane (vane B) here may perform the entire function of rocking the columella and its foot plate. However, due to the large reserve of air in the bulla, the greatest impact on this vane should occur when the turtle thrusts or retracts its head suddenly.

Thus, although the single vane in turtles is similar to the principal one in lizards, its orientation is different. Whereas in the lizards it tends to be angled anteriorly downward from a plane horizontal with the canthi of the eyes (rotated clockwise as viewed from the right in fig. 18) , it is in the turtles angled upward ten or twenty degrees (counterclockwise) . As in the lizards, the turtles are drawn with the heads in the normal position—judged from the canthi and the horizontal position of the external semicircular canal.

Vane Variations in Turtles.—Some species show deviations,

generally slight, from this pattern. *Terapene* (fig. 18) has not only the typical squamosal bulla dorsal to the tympanic cavity but another incipient bulla ventral to it in the quadrate. The side-necked turtle (Pleurodira), *Pelusios derbianus*, seems to have a definite separation of vane B to form an actual sac or bursa, opening at the surface of the drum. Although I do not have a skull of this genus, I am under the impression that it has a much reduced squamosal bulla. In such a case, air momentarily captured in this bursa may give an effective impact against the columella in response to head thrust or retraction, making up for the small bulla. I have not noted this bursa in any other form dissected.

VANE MODIFICATIONS OF THE EAR IN FROGS

The Anura as a whole do not have the vanes greatly developed. In toads they are imperfect or lacking entirely. The extrastapedial in contact with the tympanum is thick and rounded and, though it would probably have some effectiveness in intercepting air currents moving forward or backward across the inner surface of the drum, the air space itself is not very large.

In a typical frog such as *Rana* the extrastapedial seems to be definitely more vane-like in form and this is correlated with a larger drum and greater air space in this more active anuran. The same is true of *Hyla*, in which the extrastapedial is both more vane-like and is expanded against the surface of the tympanum, possibly to detect differential drum pressures when yawing in mid-air flight. This development of vanes is nothing spectacular. Only in *Rhacophorus* (*Polypedates*) *omenteimontis* (fig. 19), one of an Old World group of tree

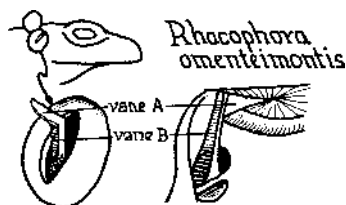


Figure 19. AIR VANES IN THE MIDDLE EAR OF THE FROG.

frogs so arboreal that it even lays its eggs in trees and is credited with being an exceptional jumper, do we see im-

proved vane character. Unlike the other frogs mentioned, the columella in this species stands away from the dorsal wall of the tympanic cavity, to which it is united for its entire length by a membranous vane corresponding to vane B in lizards. In addition the extrastapedial is more vane-like.

VANE MODIFICATIONS OF THE EAR IN SNAKES

Despite the known rapidity of movement in striking snakes, the functioning of vanes is doubtful in the Ophidia. The rodlike columella and extracolumella project posteriorly so as to contact the movable quadrate (Versluys, 1936: 763) and they appear to be suspended in a membrane (vane B) from the quadrate (*fig. 20*) but there does not appear to be a very

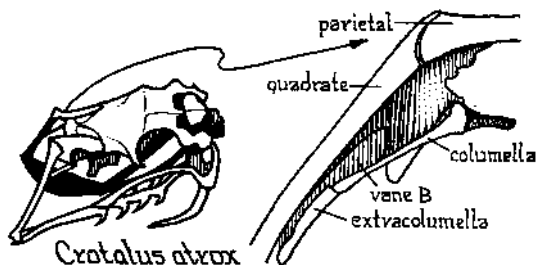


Figure 20. AIR VANES IN THE MIDDLE EAR OF THE RATTLE-SNAKE.

definite air space. True, there is some and the columella with its cartilage head has great freedom of movement. It may be that when the angle between quadrate and parietal is most obtuse as in the striking attitude (see *figs.* in Klauber, 1936), more air space would be available between the contracted muscles. A ventral hollowing out of the quadrate at its articulation with the parietal may serve to increase air space. The curving of the membrane around this depression suggests some capacity to intercept air in the forward-backward direction, though the membrane is mainly in the sagittal plane and could best detect movements from side to side. Again, as in *Basiliscus*, this vane might, doubtfully, function as a rudder.

VANE MODIFICATIONS OF THE EAR IN CROCODILIANS

While achieving its vane system differently, the Diapsida show moderate vane development. Reflecting back the skin fold which covers it (*fig. 21*), one finds a large, transparent tympanum in the alligator (*Alligator mississippiensis*). This

drum, comparable with that of a bird, is consistent with the excellent hearing of this animal, and its angle is more nearly horizontal in the skull than in any of the foregoing reptiles and amphibians. The only vane is formed by the extra-



Figure 21. AIR VANES IN THE MIDDLE EAR OF THE ALLIGATOR.

stapedial (vane A) , and it may function in trapping air against the drum in the head-turning employed in grasping prey. The opening and closing of the mouth, rapid though it is, involves mainly the lower jaw, since the skull is akinetic. Hence there is apparently no need for a complex vane-system.

FURTHER ON THE ROLE OF THE POSTULATED ACCESSORY MOTION SENSE

This section draws together ideas that have appeared in the literature and some experimental work in an attempt to test the function of the postulated accessory motion sense.

Theoretical Relation to Vision and Locomotion.—In normal locomotion the common pigeon (*Columba livia*) bobs its head back and forth in rhythm with the movement of the feet. Grinnell (1921) associated this sort of head-movement with his principle of "rapid peering"—similar to the parallax principle of astronomy, where distant objects appear to move in relation to each other when in reality the observer has moved. Stationary insects and larvae on grass blades are assumed to become more visible when the bird thrusts its head back and forth in foraging, because it is really getting binocular "fixes" with a single, laterally-placed eye, due to persistence of the after image. Each pause of the head in its forward progression provides a slightly different viewpoint. Trowbridge (1916) attempted to prove that a bird with lateral vision has great advantage over animals with binocular vision, in measuring space relations between surrounding objects, so long as it is moving.

Walls (1942: 343) has emphasized that a primary function of the eye is to detect motion, and Benner (1938) has shown the importance of shadow in defining the shape by which a seed or food-particle is recognized. He was able to deceive hens with painted kernels emphasizing shadow, while real kernels in shadowless light apparently went unrecognized.

Therefore, vision in birds is thought to be associated with head-movement, which, in turn, is co-ordinated with locomotion. If we analyze the locomotion of the pigeon, we find that it is always initiated by a forward movement of the head, followed immediately by the commencement of the first step. The head apparently reaches its most retracted position at about the instant the foot falls. Then the head is thrust forward once more, followed by forward movement of the other foot. The result, diagrammed in *fig. 22*, is a forward and

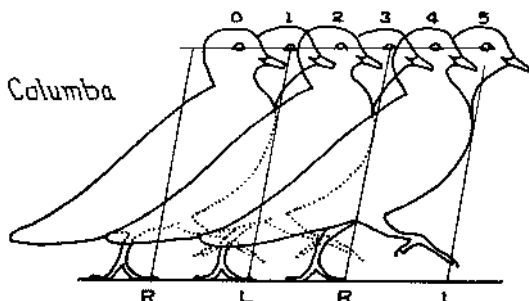


Figure 22. LOCOMOTION OF THE PIGEON. Six head positions are shown for three steps. The head never moves backward in space.

backward movement of the head for each step, or six equally-spaced visual "fixes" for three steps (left-right-left). The length of the stride is approximately twice that of the head-movement but (since the latter is forward and back while the former is only forward) the forward distance traversed by each is the same. The head *never* moves backward in space over its own track but always ahead in nearly equal abrupt "fixes."

Experimental Evidence for the Actual Role. Since the proposed motion sense supposedly reports thrust-retraction movements of the head, a simple experiment was indicated—removal of the tympanum and columella, to see if these movements are affected. This had already been done by Garnault

(1896) and Jellinek (1926) who reported no obvious effects on the behavior of the pigeon either at the time of the operation or later. To check whether the suspected new sense might co-ordinate head and limb movements, it was necessary to repeat their experiments. The tympanum and extracolumella were destroyed in a pigeon which, immediately upon release, behaved exactly as before with respect to locomotion. The nervous reflex arc, co-ordinating head-movement with locomotion, is apparently not timed by the postulated motion sense.

I then tested the reflexes of both operated and control pigeons, with special attention to the rotational experiments which Kleitman and Koppányi (1926) did on the domestic fowl (*Gallus domesticus*) Fig. 23 (after their figs. 1 and 2)

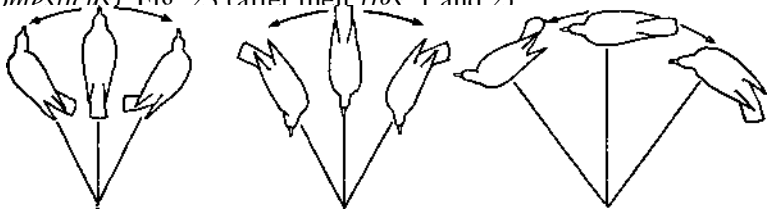


Figure 23. REFLEX RESPONSES OF BIRDS TO ROTATION. After Kleitmann and Koppányi (1926). In hand-held birds the head turning is away from the observer when the head is in the direction of the rotation, toward the observer if the tail is in the direction of rotation. The tail always turns to the same side as the head. Normal response to these tests indicates intact condition of the semicircular canals.

shows the normal reaction to these tests, though an important part of the behavior not illustrated is the head nystagmus, possibly an attempt to fix on passing objects visually. Both pigeons showed the normal reflexes, as would be expected, since the semicircular canals of the operated birds were intact.

The birds were now subjected to a movement of translation with the assumption that, if the new sense reports thrust-retraction movements, the operated pigeon should show aberrant reactions. This movement was executed at arms length, back and forth through a distance of about thirty inches—in which the head alternately faced the direction of motion and the opposite direction. Here both birds showed head nystagmus and looked about in all directions but the movement was more forced in the operated bird. Moreover, whereas the normal bird nictitated each time the head was manually

jerked forward (see Friedmann, below) , the operated one was less regular and resisted this movement actively. However, since it seemed certain that the remnant of the columella would still respond to head movements of the bird, due to its own weight and inertia, with a correspondingly near normal rocking of the foot plate in the fenestra ovale, a drastic means was taken to immobilize it. A solution of a vinyl resin (trade-name vinylseal) was introduced with a medicine dropper into the ears of the operated bird five days later, completely filling the tympanic cavity of each side.

There was a temporary response and a more permanent one following this treatment. The bird shook its head and yawned violently for the first two days, possibly a reflex reaction to fumes entering the mouth via the eustachian tubes, but this passed. The more lasting effect, also immediately noted, was a complete inability to move either the upper eye-lid or the nictitating membrane. The second bird was finally operated and its columellar stub immobilized with collodion—with precisely the same results. The co-ordination of the head-movement with locomotion was not affected in either and, after some uncertainty, both were able to feed normally on cracked corn conspicuously placed. Whether they could compete with normal pigeons in their normal environment, where food is scarcer and less conspicuous, was not ascertained.

The birds remained unable to move the upper eye-lid or nictitate, either in response to head jerking or threatening movements, raising the lower eyelid half-way only, and sleeping with it drawn up completely. At the end of two weeks I killed the second bird and determined that the collodion had, indeed, immobilized the entire columella and the fenestrae rotundum and ovale. But several days later the first bird began to recover its ability to move the upper eye-lid and the nictitating membrane—at first only a little, then more. At the end of a month it was still not normal but approaching it in this respect. At this time I killed it, also, and found that either shrinkage or gradual dissolution of the vinyl resin had progressed to a point where considerable movement of the columella was again possible.

Statistically, no conclusion seems warranted. Yet, repetition of the experiment may confirm that destroying or im-

mobilizing the columella of the pigeon has a deleterious effect upon its vision, largely through the inactivation of the upper eyelid and nictitating membrane, which are probably interdependent in action.

It should be pointed out that Dunlap and Mowrer (1930) believe that pigeons see a series of sharp, visual images, the nictitating membrane eliminating the blur which should result from head movement by passing over the cornea during the movement. According to them, the membrane is a shutter and the bird eye sees only when the head is still. Friedmann (1932) criticizes this refinement of the rapid peering principle, believing nictitation as a shutter action only coincidental. He showed that normal, hand-held pigeons nictitate when the head is jerked forward and even blinded pigeons tend to do so, though they blinked instead in half the cases. My insufficient experiments seemed to show that operating and immobilizing the middle ear as described eliminates all response of both the nictitating membrane and the upper eyelid. This may mean that the motion sense co-ordinates nictitation with head-movement in the manner suggested by Dunlap and Mowrer. The air impact on the middle ear vane with head movement would be instantaneous and, if nictitation follows at once as a reflex, the blur due to movement could be cut out.

There exists an interesting problem in that nictitation occurs only on the forward movement of the head. If it is simply a response to a jerky movement, why does it not also occur on the backward movement ? Repeated tests show that it does not, nor did Friedmann find it to do so.

The six head positions of *fig. 22* are numbered from 0 to 5. Since nictitation occurs only on the forward movement of the head, it should be noted three times, between the positions 0-1, 2-3 and 4-5. An equal advance of the head through space is also noted, however, between positions 1-2 and 3-4, but the head is being retracted between these two positions and there is not nictitation. Perhaps no nictitation is necessary because the head is advancing here at only half the body speed. We have previously noted that the head traverses the same distance back and forth as the foot does forward in the same time interval. Thus, since the head moves forward from

1 to 2 in the same time (because it is retracting) that the foot carries the body forward from L to R (twice the distance) , it has moved only half as fast through space. Its backward movement has partly cancelled the forward movement of the body.

In a further test, a jerboa (*Jaculus jaculus*) was operated through the motion tympanum of the right ear, and the auditory ossicles, sectioned at the junction of the incus and stapes. After this destruction of the linkage of the supposed air vanes with their supposed sensory receptor in the foot plate, the blind-folded animal hopped in a circle toward the left side, though it had hopped generally straight ahead in repeated trials before the operation. This is what would have been predicted. However, it was only a single specimen and it is by no means certain what else this sectioning may have affected, including the pressure in the cochlea and semicircular canals.

More refined experiments should be made by trained physiologists, using statistically adequate numbers of individuals. This paper attempts only to suggest the likelihood of the existence of an accessory motion sense, based on the functional anatomy and field observations.

Other Problems.—*Small* birds such as the house sparrow (*Passer domesticus*) do not bob the head independently. Instead, the entire body bobs along in its foraging hops. The relation of the nictitating membrane here would be interesting. It would also be simple to pierce the drum and immobilize the middle ear of the kangaroo rat to observe the effect on its jumping. It seems that the middle and outer ear play an important role in the vision of vertebrates, so vital to their food-seeking-and the associated head-movements are certainly coordinated with locomotion. I have attempted in this paper simply to interpret the mechanical behavior of the auditory ossicles and columellar apparatus in vertebrates with respect to probable air impacts on their vane-like surfaces. The nature of the reflex arc to the eyelid and nictitating membrane - if it exists—remains to be investigated.

It should be borne in mind that there is still much to be understood about the ear. The paratympanic organ, discovered by Vitali (1911-12) , is still unexplained. Many of the

head movements of vertebrates are probably partly rotational and partly linear—thus, reported by both the semicircular canals and the vanes. For this reason, it may be possible for the air vane sense to take over the functions of the semicircular canals when the latter are destroyed. Howell (1925) found that pigeons with all six ampullae destroyed eventually made a good recovery.

In conclusion, it should be said that most of the above work was done 18 years ago. At that time reptiles were not supposed to hear by sound waves at all, and the suggestion that they do so has appeared only in the last several years (Olson, 1966 Wever, et al, 1965) . Nor were the Cetacea known to use echo-location. The most recent workers on ricochetal rodents, Webster (1965) and Lay (unpublished) are confident that they are able to explain the inflated auditory bullae of kangaroo rats and jerboas, respectively, in terms of improved auditory sensitivity.

However, none of this precludes the use of the same apparatus as an accessory motion sense. We must ask why only the *ricochetal* rodents, shrews, marsupial mice and other ricochetal species all have enlarged bullae or the equivalent, if it is only for better hearing. Why do not the great numbers of non-ricochetal rodents need better hearing? Douglas Lay (personal communication) has kindly reminded me that the fat-tailed rat (*Pachyuromys*) and the jird (*Meriones*) of the Sahara have large bullae and are not jumpers—also that the marsupial mouse (*Dasyuroides*) has large bullae, yet is not ricochetal. These exceptions, two of them monotypic, should not obscure the fact that the vast majority of mammals with enlarged bullae are ricochetal.

Conceivably, these stocky types evolved large bullae with ricochetal locomotion originally, then lost the latter with change in habit, while adaptively retaining the improved ear. An analogous adaptive loss is suspected in the snow buntings (*Plectrophenax*) and longspurs (*Calcarius*) among the emberizine finches. Here the inflated occipital wing and long hind claw occur without a sign of scratching behavior. In fact these birds do not even hop as other emberizine finches do, but creep about on their bellies in a walking locomotion like that of larks, whose adaptation is imitated, convergently,

even to the straight hind claw. But this is rather clearly a secondary adaptation away from the original hopping or scratching behavior of typical emberizines. In this mouse-like seed "grazing," they eat their way forward with no *sign* of rapid peering. The few exceptions are, thus, probably explainable. Like those noted for the ricochetors above, they do not weigh heavily against the fact that the great majority of emberizine finches correlate the inflated ear region with food-scratching in the remarkable reflex described earlier. If the inflation is an aid in hearing, why do just scratchers need better hearing ? Why do just the ricochetal mammals (with the exceptions noted) need better hearing? Finally, the purposeful orientation of the middle-ear components calls for reappraisal. The additional work on the vertebrate ear in the past 18 years still leaves the above questions unanswered. The doubt remains, and it appears that not everything about the middle ear is explained in terms of hearing alone.

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